Dissertationes Forestales 263

Ecological prerequisites for successful reforestation of degraded tropical peatlands

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Academic dissertation

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Tropical peatlands of South East Asia are major hotspots of biodiversity and great carbon stores. The main peat forming ecosystem is tropical peat swamp forest (TPSF) growing on top of meters deep peat. Forest degradation by vast scale land conversions and consequent pernicious impacts on the environment have raised an urgent need for conservation and restoration. This dissertation concentrates firstly on the peat soil properties, ground surface microtopograhy and vegetation patterns of the natural TPSF, and secondly on the vegetation restoration, i.e. reforestation of degraded tropical peatland.

In the studied natural TPSF type, the forest floor can be characterized as an irregular continuum of less common hummocks and more abundant flat low-lying surface where most of the peat surface is not inundated for most of the year. Unlike in the boreal and temperate peatlands, the ground surface microtopography had no regular patterning. The surface peat structure and chemistry had differences in relation to the surface microtopography. Higher surfaces had higher nutrient concentrations and saplings and trees were concentrated on higher surfaces whereas seedlings emerge in all ground surface elevations.

In the open degraded former TPSF area we tested 21 native tree species for their potential for reforestation in a planting experiment. We increased the knowledge on the species' early stages flood and drought tolerances, species' suitability for different conditions in reforestation areas and suitable species-specific seedling height for planting. For five species with known potential for reforestation purposes we tested the impact of three site preparation treatments, weeding, fertilizing and mounding, on the seedling performance. We analyzed also the effects of wildfires which caught the study area two years after planting.

With increased knowledge on both natural TPSF ecology and the seedling experiments on degraded areas, we could specify environmental condition requirements for several tree species for reforestation.

Keywords: peat properties, microtopography, water table, restoration, peat swamp forest, site preparation, peat fires

PREFACE

First time I travelled to Borneo in 2005, I was curious and full of enthusiasm. I had promised to myself, that I will not return if I won't see an orangutan. Six weeks in the middle of jungle in good company was very much what I had expected, full of strange plants and animals and already the first day we entered the forest I saw my first orangutan, so I could use my return ticket. Every trip after that hasn't been pure bliss but through all the years I have been fortunate to work with exceptionally fine people.

My supervisors Harri and Jyrki are such people who understand the value of both careful planning and improvisation. With their experience, I have been able to avoid many hazards and mistakes they have already made before, and their continuous care has been useful, touching and funny. During the writing process of the articles and thesis, the guidance and help has been ample and invaluable, huge thanks to both! Secondly, my two companions in travels and work, in sickness and in health, Iida and Mari, you are real wonders. If Jyrki and Harri didn't take care of something, you two did. Most of all I want to thank you both for good company, in forest, office, laboratory and swimming.

Our partner in Indonesia, CIMTROP, has provided us practical help and scientific expertise, and through its late leader Suwido Limin, made the whole work in the region possible for us. We have been privileged to live within the Limin household, under the caring eye of Pak Suwido's mother. Great thanks to CIMTROP staff Kitso for managing practically everything, Siska for help with the endless bureaucracy (and being a rare female friend), Kris, Hendri, Otto, Agung, Jeni and others for sharing knowledge, hard work and crazy moments.

Then, my co-writers Sakari Sarkkola, Annukka Valkeapää, Markku Koskinen and Topi Tanhuanpää, I got the best, you have been ready for long discussions and provided insight and ideas I didn't have.

In the Department of Forest Sciences, I want to thank the whole crew, nice people I have shared room with, for all kinds of company in business and pleasure, but especially Marjut Wallner for help and positive attitude despite my serious lab-limitations during the analyses. I want to thank also Mikko Havimo for providing me his valuable thoughts and time in several long discussions and statisticians Jarkko Isotalo and late Hannu Rita for intelligent commentaries and help in statistical matters.

I have been lucky and happy to be a part of the Peatlanders community and wish that our paths will never part. I thank Kari Minkkinen for creating faith for our strength in the peat sampling and I am particularly happy for my first and oldest peat-pal Professor emeritus Juhani Päivänen who has been my support through the years.

I am grateful for the pre-examiners Prof. Susan Page and Prof. Gusti Anshari for valuable comments on my dissertation and sincere thanks to Prof. Barry Warner for agreeing to serve as my opponent in the middle of arctic darkness. I also thank the Academy of Finland, the Ministry for Foreign Affairs of Finland, the UH Faculty of Agriculture and Forestry and the Department of Forest Sciences for the financial support for my work.

Lastly, I want to thank my friends and family for being there for me in every possible way. I don't think I would have started this thesis work or science in general without my dear friend biologist Marjut Rajasilta. And my parents, your support in all aspects practical and mental has been enormous, you have never questioned basically anything I pursue.

If I forgot some of you dear ones, you are also included, Thank you!

Maija Lampela, October 11th, Helsinki

LIST OF ORGINAL ARTICLES

This dissertation is based on the following articles, which are referred to by their Roman numerals in the text. The publications are reprinted here with the kind permission of the publishers.

I Lampela M., Jauhiainen J., Vasander H. (2014). Surface peat structure and chemistry in a tropical peat swamp forest. Plant and Soil 382 (1-2): 329-347. https://doi.org/10.1007/s11104-014-2187-5.

II Lampela M., Jauhiainen J., Kämäri I., Koskinen M., Tanhuanpää T., Valkeapää A., Vasander H. (2016). Ground surface microtopography and vegetation patterns in a tropical peat swamp forest. Catena 139: 127-136. http://doi.org/10.1016/j.catena.2015.12.016.

III Lampela M., Jauhiainen J., Sarkkola S., Vasander H. (2017). Promising native tree species for reforestation of degraded tropical peatlands. Forest Ecology and Management 394: 52-63. http://doi.org/10.1016/j.foreco.2016.12.004.

IV Lampela M., Jauhiainen J., Sarkkola S., Vasander H. (2018). To treat or not to treat? The seedling performance of native tree species for reforestation on degraded tropical peatlands of SE Asia. Forest Ecology and Management 429: 217-225. https://doi.org/10.1016/j.foreco.2018.06.029.

M. Lampela is fully responsible for the summary of this doctoral thesis.
I M. Lampela planned the study together with the co-authors and executed the field work and laboratory work together with I. Kämäri and CIMTROP staff.
II M. Lampela planned the study together with I. Kämäri, J. Jauhiainen and H. Vasander, and executed the field work together with I. Kämäri and CIMTROP staff. The preliminary data processing was done by I. Kämäri for her MSc. thesis. M. Koskinen participated in the interpretation and illustration of the results, T. Tanhuanpää participated in the creation of the surface models and A. Valkeapää participated in the statistical analyses.
III and **IV** M. Lampela planned the study together with J. Jauhiainen and H. Vasander, and executed the field work together with CIMTROP staff. S. Sarkkola participated in the statistical analyses.

M. Lampela is responsible for the data analysis and overall interpretation of the results, served as the leading author, and as a corresponding author also revised each manuscript. Co-authors contributed to manuscript writing and publication process by comments on structure, substance content and by textual suggestions.

TABLE OF CONTENTS

ABBREVIATIONS

CIMTROP, Center for International Cooperation in Sustainable Management of Tropical Peatland, our research partner in Central Kalimantan, Indonesia
ENSO, The El Niño Southern Oscillation phenomenon in the Pacific Ocean causing concurrent lengthy dry periods in the South East Asian archipelago
MRP, Mega Rice project, a large scale agricultural peatland conversion and transmigration program launched by the Indonesian government in 1990's
SE Asia, South East Asia
TPSF, tropical peat swamp forest
WT, ground water table

1. INTRODUCTION

1.1. Ecological background

Tropical peatlands in the equatorial rainforest zone are intriguing ecosystems with globally important carbon stores in the soil (Lawson et al. 2015). While there are tropical peatlands also in Amazonas and central Africa in the Congo Basin, the most studied tropical peatlands with global significance to the soil carbon pool are located in South East Asia where they have gained raising attention during the last decades. The main peat forming ecosystem in SE Asia is the peat swamp forest (TPSF), which is a nutrient poor lowland freshwater ecosystem with broadleaf rainforest vegetation growing on top of peat that can be several meters deep. The TPSFs in the coastal plains of SE Asian archipelago, especially in Borneo, Sumatra and Peninsular Malaysia, have substantial soil carbon deposits developed from the vegetation remains for thousands of years (Anshari et al. 2004; Dommain et al. 2011; Biagioni et al. 2015).

Figure 1. Tropical peat swamp forest (TPSF) in the Natural Laboratory area in the Sabangau National Park in Central Kalimantan, Indonesia, seen from above from an eddy covariance monitoring tower.

The TPSFs are dome shaped, ombrotrophic, i.e. rain-water fed, peatlands often formed between two rivers with the thickest peat formations in the middle of the dome. The deepest peat found in SE Asian TPSF is 20 m deep (Anderson 1983; Melling et al. 2006). It is not clear if the natural TPSF peat stores of SE Asia are increasing nowadays but during the Holocene the few existing estimates on tropical peat accumulation rates have shown relatively fast increase: (Neuzil 1997) up to 2.5 mm $year^{-1}$ or 131 g of carbon $m^{-2}yr^{-1}$ with average long-term rate of carbon accumulation (LORCA) at 56 g of C m^{-2} yr^{-1} in one Sabangau peat core (Page et al. 2004), in comparison to the boreal and subarctic peatlands with an estimate of 18.5 g of C m^{-2} yr^{-1} (Turunen et al. 2002). The peatlands of SE Asia have an estimated area of 25 million hectares and carbon store of 52 Gt, which equals at least 10% of the estimated global peat carbon store (Page et al. 2011).

The main vegetation in TPSF consists of trees (Fig. 1) and the peat is thus formed of woody debris. Thick rain forest vegetation with up to 40 m tall trees (MacKinnon et al. 1996) creates shaded conditions and a fairly stable microclimate under the canopy. A distinctive feature in the TPSF is the undulating uneven ground surface microtopography with frequent higher and lower surfaces, namely hummocks and hollows (Shepherd et al. 1997; Shimamura and Momose 2005). Most of the year the ground water table (WT) is close or above the soil surface inundating the hollows, but the seasonal WT differences may exceed 1 m within one year (Takahashi et al. 2002). The input of nutrients to the ecosystem comes only from rainwater and through dry deposition from the atmosphere and the rest of the nutrients supporting vegetation growth are freed from decomposing organic matter. In ombrotrophic TPSF forest floor, the limited nutrient pool in peat (Könönen et al. 2015; 2016), acidic conditions and high water table that keeps soil in anoxic conditions, reduce the decomposition rate favoring peat accumulation further (Page et al. 1999; Weiss et al. 2002).

Figure 2. A carnivorous pitcher plant *Nepenthes ampullaria* in the flooded forest floor in the Natural Laboratory in the Sabangau National Park.

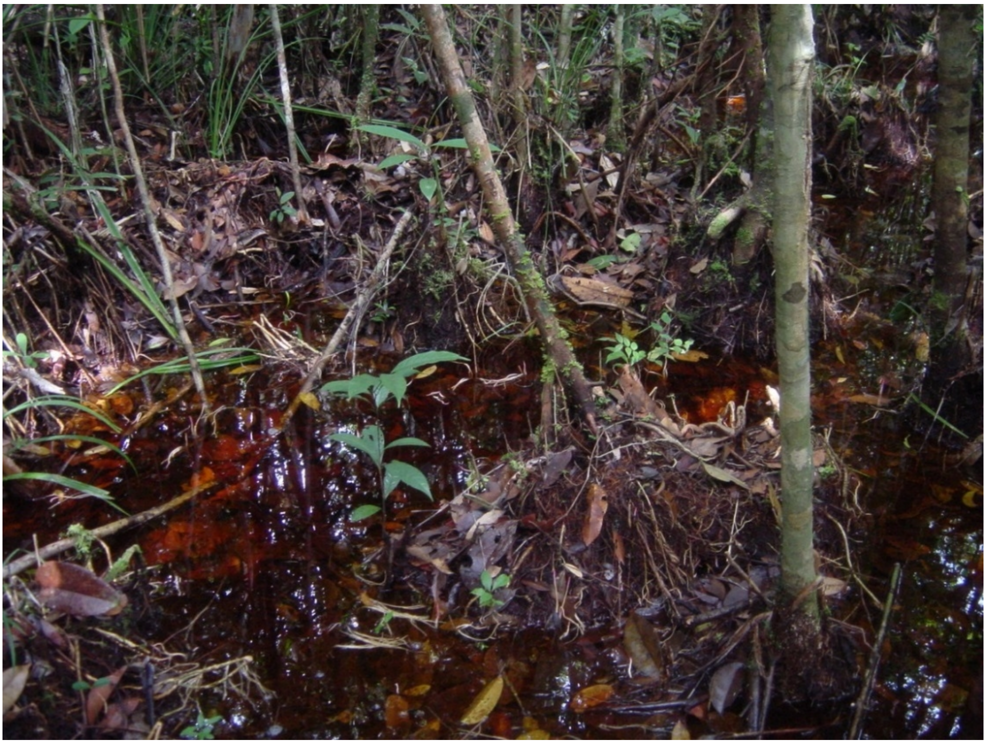


Figure 3. TPSF forest floor with typical vegetation consisting of trees, tree seedlings and pandans (*Pandanus sp.*) during the wet season in the Natural Laboratory in the Sabangau National Park.

Similarly to the tropical rain forests on mineral soils, TPSFs of SE Asia have high biodiversity exemplified by the still relatively viable populations of high conservation status mammals, such as orangutans, in Sumatra and Borneo (Husson et al. 2009). The diverse floral communities of SE Asian TPSF can contain more than 150 tree species within one forest area (Waldes and Page 2002), abundance of epiphytes and climbers, and such specifically to the nutrient poor conditions adapted features as the carnivorous pitcher plants (Fig 2). In TPSF, the forest is dense with reported averages of ~2700 (DBH diameter at breast height > 4.7 cm) and ~2000 (DBH > 7 cm) trees per hectare (Mirmanto 2010; Kronseder et al. 2012, respectively), and the forest floor is covered with tree seedlings and saplings.

In general, we may assume that the trees of TPSF need to be adapted to periodically high WT level, low light, low nutrient availability and soft peat as growing media (Fig. 3). To overcome the anoxic conditions in peat formed during the high WT level, some tree species have pneumatophores that conduct air to the roots (Fig. 4). Hummocks and hollows in the forest floor provide different microhabitats for species with differing tolerance for high WT and anoxic conditions (Freund et al. 2018). We may assume that most of the TPSF tree species are adapted to low light also in the early stages, but tree mortality creates gaps in the canopy-cover and alters the light conditions as well as adds opportunities for competition for space and nutrients for more light demanding species. Gaps are often fast occupied by pioneer

Figure 4. Forest floor in the dry season in the Sabangau National Park showing knee and stick shaped pneumatophores that are able to conduct air to the roots during flooding.

vegetation such as thorny pandan thickets (*Pandanus* sp.). The nutrient uptake by trees is enhanced by symbiosis with mycorrhizal fungi (Tawaraya et al. 2003). As adaptations to the soft soil, many tree species have large supportive root formations such as stilt roots and plank roots. Species level knowledge on these traits is nevertheless sparse, as the TPSF tree species and their ecology is very little studied and there are still gaps in the taxonomical knowledge (Graham et al. 2017).

1.2. Land use change in tropical peatlands of SE Asia

Because of the rugged conditions and remote locations, the TPSFs of SE Asia have only fairly recently become better known and thus also exploited in large scale. The first major development target in TPSF was during the last years of 1990's when Indonesian government launched the Mega Rice project (MRP) in the province of Central Kalimantan (Notohadiprawiro 1998). By the year 1997, nearly 1 million hectares, largely in pristine TPSFs, were drained with 4000 km long canal network. The purpose was to introduce new areas for rice cultivation and other agriculture by transmigrants moving to the area from overly populated Indonesian regions. The El Niño Southern Oscillation (ENSO) phenomenon in the Pacific in 1997 caused prolonged draught in the area and vast areas of the MRP caught fire. The fires lasted for months and during the next few years it became clear that most of the project area was not suitable for rice cultivation or other agriculture due to poor soil characteristics for agriculture and difficulties in water management. The tension between the local people and the transmigrants ended in violent conflicts in the year 2001 (ICG 2001) and the project area became largely abandoned wasteland with recurring fires (Boehm and Siegert 2001). Already by the end of 1990's, the poor situation had been acknowledged both by many of the Indonesian officials and the international scientific community. Since then, several research and practical restoration projects have been conducted in the area and knowledge on both ecology and restoration technology has increased (e.g. Jauhiainen et al. 2008; Giesen 2009; Page et al. 2009; Ichsan et al. 2013; Ritzema et al. 2014; Graham et al 2017). Most of the former MRP area still prevails in degraded state as well as increasing areas of TPSF in the whole SE Asia (Dohong et al. 2017).

The progressive land conversion to agriculture, but most importantly to palm oil and pulp wood plantations, has been rapid during the last two decades. Unclear land tenure and wide spread corruption have eased the initiation of unsustainable commercial ventures that have had no interest in the long-term feasibility of their land-use (Evers et al. 2017; Wijedasa et al. 2017). In practice this means vast abandoned clear-cut and drained areas that have sparse secondary vegetation (Fig. 5 and Fig. 6). These open peat areas are prone to fires and thus recurring fires have deepened the severity of the degradation (Fig. 6). In 2015, only 6 % of

Figure 5. View straight after fires in year 2009 at Mega Rice Project area near Kalampangan village in Central Kalimantan. Ferns *Pteridium aquilinum* and *Stenochlaena palustris* sprouting.

the original TPSF area in Peninsular Malaysia, Sumatra and Borneo remained in pristine state while 50 % was industrial plantations and small-holder dominated areas, and 20 % was classified as open undeveloped, degraded land (Miettinen et al. 2016).

Open degraded several times burnt peat areas, such as the majority of the MRP area (Fig. 5) with continuing uncontrolled draining have several unfavorable conditions forming barriers to ecosystem recovery and forest regeneration (Fig. 6): 1) diminished litter input to the soil from the reduced amount of vegetation and thus diminished organic matter supply supporting peat accumulation, 2) diminished nutrient input due to the reduced amount of decomposing litter, 3) continued leaching of the nutrients from the surface peat that is impacted by the annual WT changes and exposed to heavy rains (Könönen et al. 2015), 4) the surface peat in oxic conditions compacts, decomposes and results in lowering of the soil surface and increase in flood-prone surfaces during rainy season (Konecny et al. 2016), 5) with effective uncontrolled drainage and without full protecting canopy cover, the WT fluctuation is more extreme than in the pristine forest causing flooding during the wet season and excessive dryness in surface peat during the dry season (Hirano et al. 2015; Jauhiainen et al. 2008), 6) higher diurnal peat temperature variation in comparison to the pristine TPSF (Jauhiainen et al. 2014), 7) limited amount of vegetation, higher daytime air temperatures and higher susceptibility to winds induce dryness and increase the susceptibility to fires (Miettinen et al. 2012), 8) limited supply of seeds and seedlings for natural forest regeneration (Blackham et al. 2013; 2014), 9) harsh open conditions for seedlings adapted to the stable humid microclimate and low light of the forest may reduce seedling survival, 10) loss of the natural microtopography limits spots for habitat differentiation (Freund et al. 2018), 11) loss of floral biodiversity with very limited number of species causing disturbance in the successional pathways (Graham et al. 2017), and 12) loss of mycorrhizas that are vital associates in nutrient uptake of several plant species (Turjaman et al. 2006; 2011; Graham et al. 2013).

The parts of the degraded TPSF area that have been taken into cultivation, have in addition to the above mentioned even more wide-ranging set of problems. Firstly, peat as substrate is very nutrient poor and acidic for agricultural crops and oil palm and needs constant fertilizing which likely also speeds up the peat decomposition process. Secondly, in the shallow coastal peat areas, if the peat subsidence due to drainage further continues, the widely found acid sulphate deposits below the peat can acidify the soils and waters if exposed to oxic conditions. This as well as salt water intrusion in the coastal areas effectively prohibit all further cultivation. Lastly, the use of fire for land clearing and soil amendment and also common recklessness with fire handling have caused fire hazards that have spread to vast areas during the driest periods (Cattau et al. 2016). It is estimated that in Peninsular Malaysia, Sumatra and Borneo, the yearly carbon emissions in 2015 from peat oxidation with different land use types ranged between 132.2 Mt C yr^{-1} and 159.2 Mt C yr^{-1} whereas the yearly fire induced carbon emissions over the past ten years average at 122.1 Mt C yr^{-1} (Miettinen et al. 2017). Haze from the fires has covered extensive areas in SE Asia with severe consequences to people's health more often in recent years (Koplitz et al. 2016).

It appears, that tropical peatland system is able to accumulate sufficiently fast carbon to compensate carbon losses in decomposition in soil, and thus sustain its soil carbon stores, only in natural state as TPSF (cf. Miettinen et al. 2017). The recent development with intensifying fires has caught both local and international attention and TPSF restoration has reached increasing interest (Wijedasa et al. 2017). In 2015, the fires were estimated to be wider spread and more severe than before. This led to political consensus in the country of the highest area of TPSF in SE Asia, Indonesia, to ban the future development of tropical

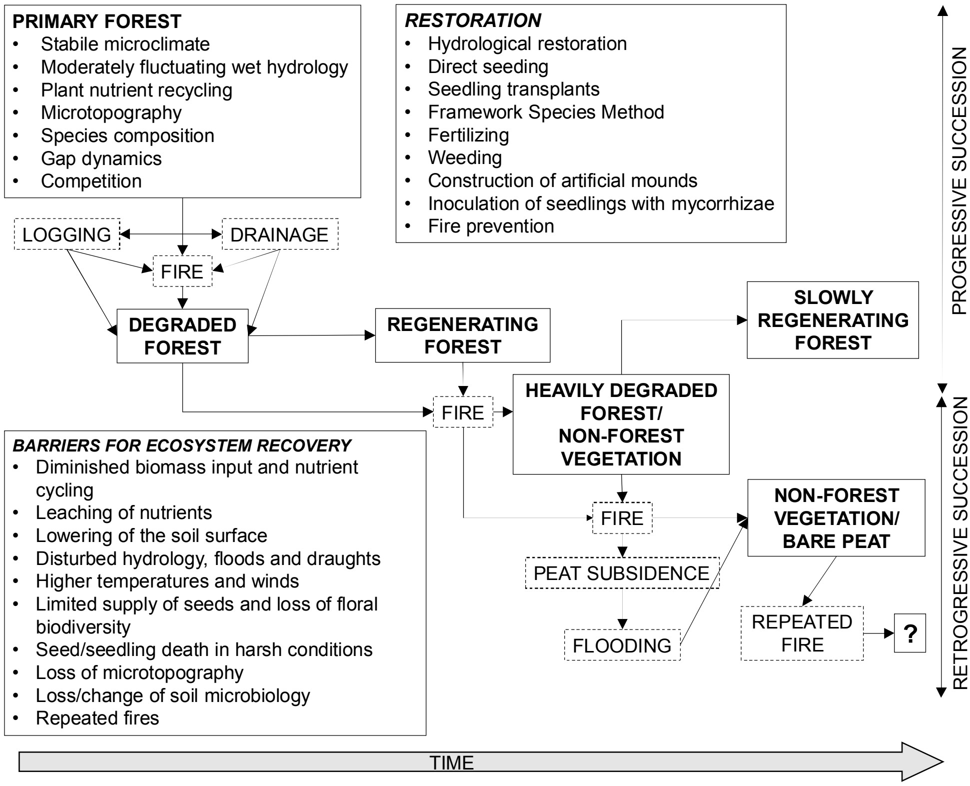


Figure 6. Pathways to degradation and restoration of TPSF. Modified from Page et al. 2009 and Graham et al. 2017.

peatlands and endorse rewetting and reforestation of the drained areas (Minister of Environment and Forestry 2015), and in January 2016 Indonesian government launched a peat restoration agency (BRG) straight under presidential govern. The target set for BRG was to restore 2 million hectares of degraded TPSF within 5 years. This act has boosted the activities and financing within restoration in the region (Hansson and Dargusch 2018), but the results are yet to be verified.

1.3. Restoration of tropical peatlands

In general, the target in restoration of ecosystems is to get back the original functions and species composition of the ecosystem (Clewell and Aronson 2013). In complex ecosystems, such as tropical rain forests, with diverse interspecies relations and feedback mechanisms between the environment and species, it is not likely for secondary forests or vegetation restoration (i.e. reforestation in the case of forests) to reach the original biodiversity (Gibson et al. 2011). Therefore, for biodiversity conservation, leaving tropical forests intact (in this case TPSF) should be the priority of nature conservation (Posa et al. 2011). If this is not possible due to reasons such as widely spread degradation, patchiness of natural forests or land tenure conditions, and there is a need for ameliorating the environmental conditions, restoration of the degraded ecosystems becomes increasingly topical. In degraded tropical peatlands, restoration can potentially strengthen ecosystem viability and regain peatland's functions as carbon store sustaining system, as well as provide numerous ecosystem services, such as fresh water storage, regional climatic regulation functions and source for non-forest timber products (Giesen 2015; Osaki and Nobuyuki 2016).

Based on research in several continents and biographical regions, the main ecological factors predicting forest restoration success are the time since restoration and the type of disturbance (Crouzeilles et al. 2016). This means, that in forest ecosystems where reaching full canopy forest may take decades, the restoration success can be judged only after substantial amount of time, and lower level of the original degradation predicts better restoration outcome. In the degraded tropical peatlands, the need for restoration has been acknowledged only fairly recently (Page et al. 2009) and the level of degradation is high with vast areas of treeless and recurrently burnt peatlands. There is thus by far very little large-scale or long-term experience in the restoration of these systems gained in projects run by governmental bodies, NGO's and research projects (Page et al. 2009; Graham et al. 2017).

When restoring degraded TPSF there are several aspects to take into account (Fig. 6). To initiate the development towards functioning TPSF ecosystem, the first target is to stop the effective drainage of the area. This means usually blocking the drainage ditches and larger canals with dams. In practice this has proven to be very demanding in the most heavily degraded areas such as the MRP area due to the big size of the canals, high amount of water during the wet season and lack of experience in technical solutions for durable dam construction in soft peat (Ritzema et al. 2014). Ritzema et al. (2014) also noted that despite effective dam structures built in the experiment, the hydrological conditions were improved but the WT still dropped to 1 m depth below the soil surface towards the end of the dry season. Hydrological restoration may thus require intense and expensive structures and despite all the efforts have limited impact in the restoration process. Nevertheless, it is expected that hydrological restoration will keep the WT higher during the dry season and thus reduce the susceptibility to fires in the area (Jaenicke 2010). If hydrological restoration is not possible, in some areas one option may be to start only with vegetation restoration that could (if fires can be avoided) at some point start maintaining higher WT and regain other ecosystem functions. Natural regeneration in the rewetted areas may not be sufficient for vegetation recovery (Blackham et al. 2013; 2014), therefore vegetation restoration with either direct seeding or by planting seedlings may be needed. As in reforestation in general (Clewell and Aronson 2013), the focus should be in native species and special attention should be paid on the species selection. In this, if existing literature on the species is limited, local knowledge on species uses and ecology can be valuable. Framework species method, which involves planting a mixture of local species with differing traits (pioneer and climax species, economically important, etc.) and with ability to rapidly launch the ecosystem recovery, can be a useful tool in planning the reforestation (Blakesley et al. 2002; Graham et al 2017). Techniques for enhancing vegetation recovery and seedling recruitment such as fertilizing, weeding and mounding can be considered. Inoculating the seedlings with suitable mycorrhizae before planting has also proven to be, in some cases, beneficial for seedling success (Turjaman et al. 2011; Graham et al. 2013). Lastly, the local experts and communities should be engaged in the TPSF restoration in such ways, that the fire hazards mostly caused by human can be avoided and benefits from avoided fires can be indicated. This can be implemented as education on sustainable use of fire, fire-fighting education, and creating a feeling of ownership to the restoration area by securing land tenure. As TPSF restoration is a long-term task and needs monitoring, possible interventions for continued progress and often fire prevention, there may be a need for continued financing.

1.4. Scope and motivation

This PhD work is a combination of four studies conducted in the TPSFs in Central Kalimantan, Indonesia. First two articles concentrate on the soil and ground surface properties of the natural TPSF and form a background for the last two articles concentrating on the reforestation of degraded TPSF. In the first article (I) we studied the surface peat physical and chemical properties of a natural TPSF. The second article (II) concentrates on the ground surface microtopography and vegetation patterns of the natural forest. In the third article (III) we studied the tree species suitable for degraded TPSF reforestation with a seedling planting experiment of 21 species. In the fourth article (IV) we further studied the tree seedling performance on degraded TPSF of five selected species with three different site preparation treatments. All these four studies aim at increasing ecological knowledge of the TPSF for the purposes of TPSF conservation and restoration.

2. MATERIALS AND METHODS

2.1. Study areas

All the four studies were conducted in either natural or degraded TPSF in Central Kalimantan, Indonesia near the provincial capital Palangka Raya (Fig. 7). The area is 200 km inland north from the Java sea and dominated by flat terrains and peat soils with ground elevation at highest 40 m.a.s.l. Data for the first two studies were collected in a natural peat swamp forest in Sabangau National Park in the so-called Natural Laboratory area (2°20’ S, 113°55’ E) west from river Sabangau. For the third study, the data was collected both in the Natural Laboratory area and near village Kalampangan in the former MRP area block-C on degraded former peat swamp forest (Kalampangan area, 2°20' S, 114°01 E) between the rivers Sabangau to the west and Kahayan to the east. For the fourth study the data was collected in Kalampangan area. Both these areas are managed by the Center for International Cooperation in Sustainable Management of Tropical Peatland (CIMTROP) and are reserved for research purposes.

The mean annual precipitation in the area is approximately 2500 mm yr-1 and the temperature is fairly constant with yearly average approx. 26°C (Hirano et al. 2014). The area belongs to tropical rainforest climate zone. The local climate has a drier season starting in July – September and ending at latest in November with wide interannual variation both in the length of the dry season and the amount of precipitation. During the last decades, the ENSO phenomenon has strengthened causing prolonged and more often recurring dry periods in the area.

The Natural Laboratory area (I, II, III) has been selectively logged during the 1900s with operations ending by 1997. The effects of the logging can still be seen as a relative abundance of younger trees especially near the river and with gradual increase in proportion of big trees towards the interior of the forest. Small canals dug for illegal timber transport still drain the peat dome to certain extent, but much of the canals were already filled with organic residue or dammed as conservation measures during the study. Between the forest edge and the dry season river course lies up to 2 km wide flat degraded floodplain (III, Fig. 8). This former riverine forest is nowadays open seasonally inundated area with sedges, reeds, grasses, and pandans (*Pandanus sp.*) and bushes such as *Ploiarium alternifolium* (Vahl) Melch., *Syzygium claviflorum* (Roxb.) Wall. ex A.M.Cowan & Cowan and *Syzygium zeylanicum* (L.) DC. The whole Natural Laboratory area is thus not in pristine state. It has nevertheless maintained many of the natural characteristics including viable wildlife and flora that contains several endemic and endangered species. Inside the forest (I, II), the main vegetation consists of trees that form several canopy layers with the tallest trees reaching 35 m (Page et al. 1999). Common genera in the Natural Laboratory area are Clusiaceae, Sapotaceae, Myrtaceae, Rhizophoraceae, Dipterocarpaceae, Polygalaceae and Euphorbiaceae, and common species *Palaquium leiocarpum* Boerl., *Combretocarpus rotundatus* (Miq.) Danser, *Syzygium densinervium* (Merr.) Merr., *Calophyllum teysmannii* Miq., *Xanthophyllum palembanicum* Miq. and *Gonystylus bancanus* (Miq.) Kurz (Mirmanto 2010). The forest floor consists of tree roots, decaying wood and leafs, and several types of aerial roots and air conducting root structures, pneumatophores. The ground vegetation consists mostly of tree seedlings and pandans that occupy open gaps formed by fallen trees. The peat depth varies from shallow peat near the river up to 12.6 m deep peat deposits in the middle of the peat dome (Shepherd et al. 1997). In the Natural Laboratory study sites, the peat depth varied from 1.5-2.2 m inside

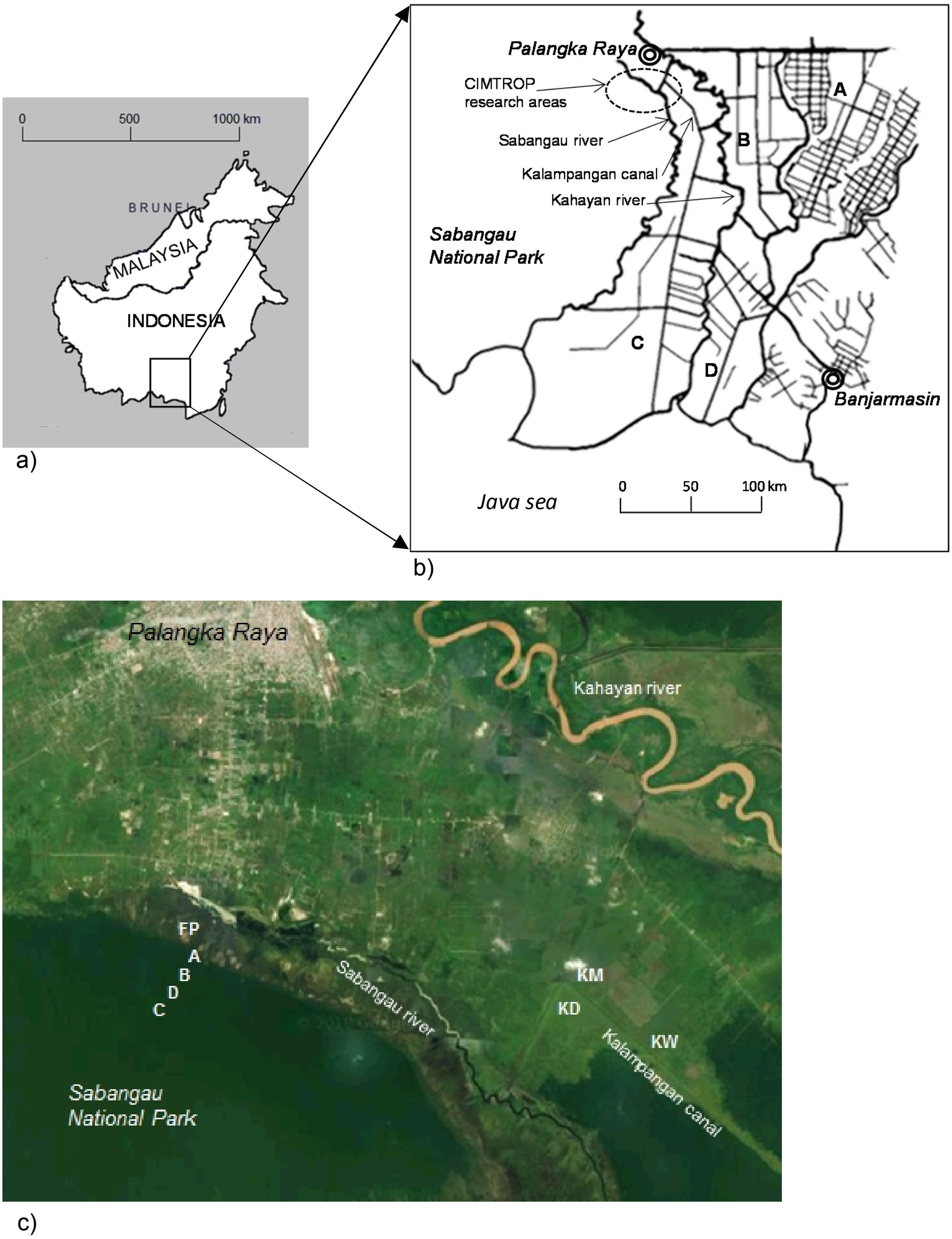


Figure 7. a) Island of Borneo in South East Asia, **b)** Area of Central Kalimantan in Borneo Island from Java Sea down to provincial capital Palangka Raya on the top with CIMTROP research areas, Mega Rice Project (MRP) canal network, blocks (A, B, C and D) and main rivers draining to the Java Sea from left: Sabangau, Kahayan, Kapuas and Barito, **c)** Research sites near Palangka Raya managed by CIMTROP: Natural Laboratory area on the left with floodplain (FP) and plots A, B, C and D inside the forest; Kalampangan area on the right with dry (KD), middle (KM) and wet (KW) blocks near the junction of the two drainage canals (googlemaps).

a)

b)

Figure 8. a) Open floodplain of river Sabangau in the Natural Laboratory during the dry season and a rail track leading to the Natural Laboratory basecamp inside the forest. Vegetation consists of sedges, reeds, grasses, pandans (*Pandanus sp.*) and bushes such as *Ploiarium alternifolium, Syzygium claviflorum,* and *Syzygium zeylanicum.* **b)** Same place during the wet season. CIMTROP staff member Jeni Richardo entering the forest edge with boat.

the forest (I, II) to 1.2-2.0 m in the forest edge and open flood plain (III). Inside the forest (I, II), the soil surface has typical microtopogaphy of TPSF consisting of drier hummocks and hollows often filled with water during wet season. Air temperature stays fairly constant inside the forest throughout the year with yearly mean between 25°C and 27°C and the diurnal changes are small.

The Kalampangan area (III, IV) is a former TPSF which has been drained with canals up to 25 m wide and 8 m deep during the MRP. The forest is clear-cut and the terrain has burnt several times. Floral diversity is low in comparison to natural TPSF and some patches remain without any vegetation exposing bare peat. Vegetation consists mainly of ferns (e.g. *Pteridium aquilinum* (L.) Kuhn, *Stenochlaena palustris* (Burm. f.) Bedd. and *Polypodium sp.*), sparse bushes (e.g. *Ploiarium alternifolium, Melastoma malabathricum* L. and *Ficus deltoidea* Jack) and stunted trees (e.g. *Combretocarpus rotundatus*, *Cratoxylum glaucum* Korth., *Cratoxylum arborescens* (Vahl) Blume and *Acacia crassicarpa* Benth.). In the study plots the peat depth is approximately 4 m. The original microtopography is lost and the soil surface is mostly very flat with occasional burnt depressions. The surface peat has lost most of its plant nutrients and the peat is compacted (Könönen et al. 2015). The open soil surface is predisposed to wide diurnal changes in temperatures (from 24°C to 36°C in 5 cm depth), and the mean temperature close to surface (28.9 ± 2.4°C) as well as air temperatures are higher than in the forest environment (Jauhiainen et al. 2014).

2.2. Experimental designs, data collection and analyses

2.2.1. Natural laboratory peat profiles, microtopography and vegetation

Study plots in the Natural Laboratory (I, II) were chosen outside the river flooding zone in the mixed swamp forest type (MSF, described in Page et al. 1999). In this forest type the annual differences in the WT are typically wide up to 1 m and hummocks and hollows are common features in the forest floor. Three plots were chosen from plots used in previous research (plots 0 and 1B in Shepherd et al. (1997); Page et al. (1999); Waldes and Page (2002) and transect 2.25 km used by CIMTROP and Borneo Nature Foundation for vegetation and animal surveys), namely plot A, B and C, situated 250 m, 800 m, and 2500 m from the edge of the forest and the Sabangau river flooding zone, respectively. For article II we established one additional plot, between plots B and C, namely plot D, 1600 m from the forest edge (Fig. 7).

In plots A, B, C and D, we established two 50-m-long transects in each plot, to study the ground surface elevation differences: one towards the center of the peat dome against the common water flow direction and another in perpendicular direction, altogether eight transects. From the transects, we measured ground surface elevation approximately once in every 25 cm distance and recorded the WT when present. Occurrence of vegetation divided into trees (DBH > 5 cm), saplings (DBH 2-5 cm), seedlings (DBH < 2 cm), pneumatophores and pandans was recorded within 25 cm distance of the center line from both sides of the transect. For estimating whether the microtopographical patterns on the forest floor where related to the water flow direction, we compared the differences in the frequency of elevation changes in transects in relation to the transect direction. To study the change in vegetation from the forest edge towards the center of the peat dome, we compared the amount of different types of vegetation between the plots.

To study the microtopography in detail and collect surface peat profile samples, in plots

A, B and C, three 3.9 m x 3.9 m subplots (except plot 1 in site A was 5.1 m x 5.1 m) were established along the transects, altogether nine subplots. From each subplot, we recorded ground surface elevation and WT and located vegetation in detail from a grid of 30 cm x 30 cm. The peat depth in each subplot was measured by using a Belorussian peat corer. From the elevation data, we created digital elevation models for illustrations and spatial analyses and added vegetation data to the models.

After this, we selected locations for peat sampling so, that equal number of higher surfaces (hummocks) and lower surfaces (hollows) were chosen. We took altogether 24 surface peat profiles to 70 cm depth, 12 from hummocks and 12 from hollows with a box-shaped steel peat corer (Pitkänen et al. 2011), 8 from each plot (A, B and C). The ground surface elevation of the profile was defined based on the grid elevation measurements. Undecomposed litter was separated from the surface of the profiles and stored. Each profile was divided horizontally into 1-7 samples based on visually observed differences in the peat structure. The degree of decomposition was measured in the field with the von Post method (von Post 1922). In the laboratory, we measured the unrubbed fiber content (Soil Survey Staff 1999) of the peat and separated living roots from the samples. Litter, roots, and peat were dried for dry mass determination. Total element concentrations and ash content were determined from dried and homogenized material. We divided the peat property data into four categories based on the sample's vertical location in the forest floor to illustrate the differing conditions on the forest floor: litter, hummock surface, hollow surface, hollow bottom. The differences between the categories were tested with Kruskal-Wallis test and further with Jonckheere-Terpstra post hoc test.

The ground water table was monitored several times in the subplots and transects from plastic pipes installed at the beginning of the measurement period. This manually collected data was then compared with automated long-term logger data available from plot B (provided by Dr. Hidenori Takahashi). To investigate the patterns in WT in natural forest, we used logger data from the years 1999 to 2005 excluding the exceptionally dry year 2002. WT median calculated from this data was chosen to represent the typical WT level and was thus chosen as 0-level WT and ground surface level.

Data were collected in March–April 2005 during the wet season when the forest floor was flooding so that the microtopography was easily observed as hollows were water-inundated and part of hummock surfaces were above the water surface.

2.2.2. Seedling experiments and site preparation treatments

In Kalampangan area (III, IV), we established three blocks on locations with differing WT conditions: dry block with almost never visible WT, frequent burnt depressions and patchy low vegetation consisting mostly of ferns; middle block with very flat soil surface and low vegetation consisting of ferns and sparse bushes; and wet block that had occasionally thick bush vegetation and most of the year water-filled depressions.

We chose 21 local tree species to test their potential for reforestation on degraded peat (species listed in the article III). Most of these species had either some value as non-wood forest products for local people or they had shown some potential in former reforestation trials. Seeds were collected from local forests and seedlings were grown in a field nursery in the Kalampangan area for 6-11 months before planting. In November 2012 at the beginning of the wet season, the seedlings were planted in the three blocks in 9 x 9 m plots with 1.5 m planting distance (6-36 seedlings per plot depending on the seedling availability) with one species per plot. No site preparation was executed (Fig. 9).

Figure 9. Degraded several times burnt former TPSF in Kalampangan area, dry block. Vegetation consists mainly of ferns (*Pteridium aquilinum, Stenochlaena palustris, Polypodium sp*.) sparse bushes of *Ploiarium alternifolium, Melastoma malabathricum* and stunted trees such as *Combretocarpus rotundatus*, *Cratoxylum glaucum* and *Acacia crassicarpa*. Measuring the soil surface elevation and seedling height during planting in November 2012 in a non–weeding plot. Field assistants Riyanto and Riyadi.

For five selected species (IV), *Shorea balangeran* Burck, *Alstonia pneumatophora, Dyera polyphylla* Baker ex Den Berger, *Dacryodes rostrata* (Blume) H.J.Lam and *Campnosperma squamatum* Ridl., with known potential for reforestation (Takahashi et al. 2001; Van Eijk et al. 2009; Graham 2009; Wibisono and Gandrung 2008), we performed three different treatments: weeding in three categories (no weeding, moderate weeding and total weeding), fertilizing (0/1) and mounding (0/1), one treatment or combination of treatments per plot.

We monitored the seedling height at 12-week intervals and survival at 4-week intervals for one year, then once 1.5 years after planting (Fig. 10). In September 2014 wildfires caught the Kalampangan area and damaged all the blocks with varying intensity. The Kalampangan plots were measured once more after the fire damage approximately two years after planting (III, IV).

WT was monitored in each block with automated loggers with one hour intervals and manually from plastic pipes with two weeks intervals. Blocks were leveled and for WT comparisons between the blocks, we used synchronized logger data from the blocks. Surface elevation of every planted seedling was also leveled. The soil temperature in mounds and ground surface in 5 cm depth were monitored with automated loggers storing readings once every hour.

To study the effect of environmental factors (III, IV) and treatments (IV) on seedling growth, we used linear mixed modelling, where the effects of interest are expressed as fixed parameters and other effects that derive from the sampling or other external factors are expressed as random parameters (following West et al. (2014) procedure for clustered longitudinal data). The selected fixed variables were WT, dry season, wet season, seedling height at planting, age of seedling (III, IV), weeding, fertilizing and mounding (IV). The random part of the models consisted of intercept for each individual seedling and two-parameter autoregressive (AR1) covariance structure that takes into account the correlation between the repeated measurements. To study the effect of environmental factors (III, IV) and treatments (IV) on seedling survival, we used Cox proportional hazard regression modeling (Cox 1972) with similar variables as the fixed variables in the growth models. We created a growth and a survival model for each species and included in the model only those fixed variables that derived significant results.

Figure 10. Measuring the height of a *Shorea balangeran* seedling in Kalampangan area in the middle block in a mound built from plastic fabric and filled with peat soil during the wet season in February 2013. CIMTROP staff member Jeni Richardo.

a)

Figure 11. Natural Laboratory floodplain transect measuring in February 2013 during the wet season. **a)** Near the forest edge searching for the plastic WT measurement pipes underwater, CIMTROP staff member Kris Yoyo steering the boat. **b)** Inside the forest edge searching for seedlings underwater, CIMTROP staff member Jeni Richardo.

b)

Figure 12. Natural Laboratory floodplain inside the forest edge during the dry season. CIMTROP field manager Kitso Kusin and Jyrki Jauhiainen.

The effects of the fertilizing on the seedling biomass and biomass allocation were studied in two species: *Shorea balangeran* and *Alstonia pneumatophora* (IV). After 14 months of growing in the plots, the seedlings were dug out and separated into biomass fractions: roots, stem and leaves. Leaves were photographed, the leaf area was calculated with imaging software and the biomass fractions were dried and weighed for dry mass determination.

Also in November 2012 (III), in the Natural Laboratory, we established two transects in the river floodplain starting from inside the forest from the point that is out of river water flooding and ending in the open degraded area along the elevation gradient down towards the river (Fig. 11 and 12). We leveled the ground surface elevation and planted seedlings of 6 species (altogether 240 seedlings) in 20 perpendicular rows along the transect so that each row was 5 cm lower in elevation than the previous one. Hence the elevation difference between the highest and lowest elevation was 1 m and the lengths of the transects were approximately 200 m. Seedling height and survival were monitored following the similar schedule as in the Kalampangan experiments. WT was monitored from plastic pipes (5 along each transect) and from an automated logger established near the lowest lying seedling row in the open floodplain.

3. RESULTS

3.1. Natural TPSF forest floor structure and water table

In the Natural Laboratory forest (I, II), the forest floor structure was very uneven and no consistency in the hummock-hollow variation could be observed. The forest floor was covered with leaf litter and other woody debris piling on top of tree roots, fallen tree trunks, rotten stumps and clumps of pneumatophores forming irregular hummocks. Hollows in between were either slightly lower surfaces of deeper holes in places of uprooted fallen trees. The corings taken with the Belorussian peat corer revealed several burnt layers in the peat.

The annual WT changes in the forest floor were approx. 1 m within the 4 years logger-data measurement period with mean WT in -7 cm (0 cm level set to the median WT). The extreme low and high WTs were short in time as 90 % of the time the WT was above -41 cm and below +15 cm from the 0-level (Fig. 13).

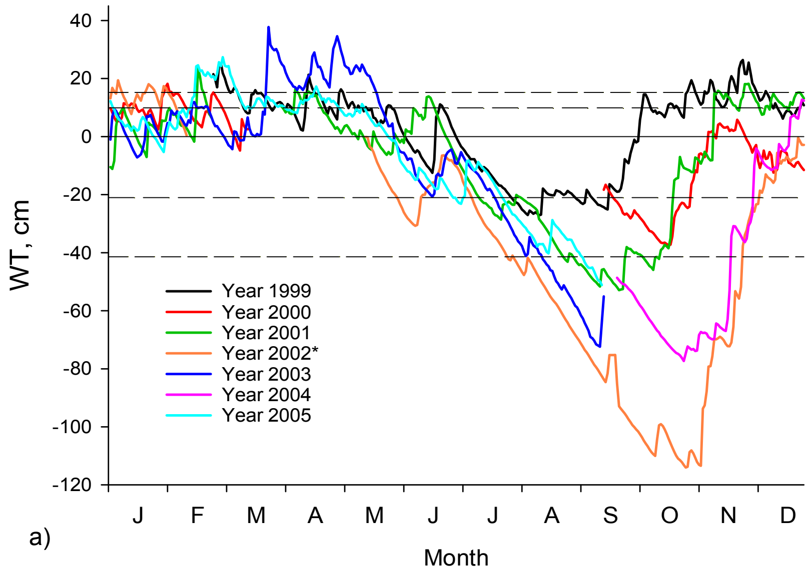
3.2. Peat structure and chemistry

The peat profiles (I) taken from hummocks and hollows revealed great variation in the observed physical peat properties. The peat structure varied from coarse and undecomposed to fine structured and highly decomposed. Some samples in the plots nearer the river contained layers of charcoal and some a lot of living roots. The variation in BD values was high and ranged from 0.013 to 0.197 g cm^{-3} with very low values in the hummock surfaces. Degree of decomposition as well as bulk density values increased downwards in the peat profiles.

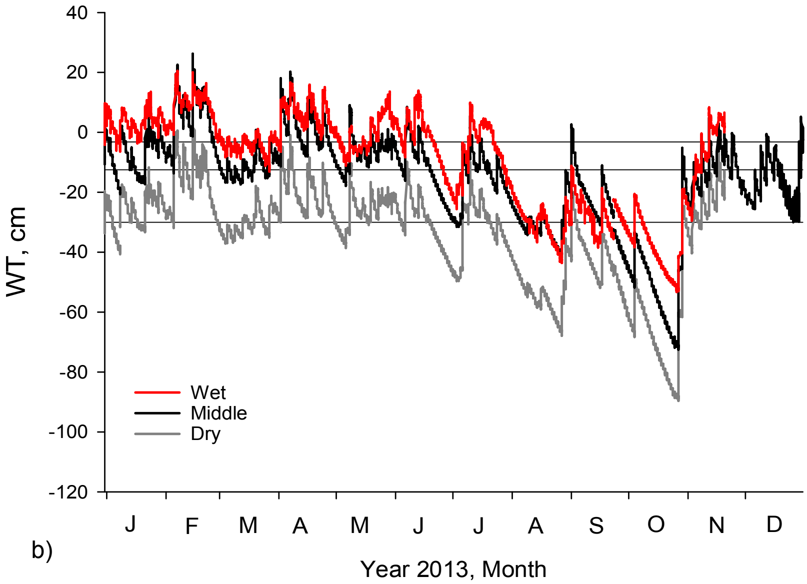
The amount of mineral nutrients and ash were very low in the peat samples with decreasing values downwards in the peat profile. The mean carbon content was 57 % and the carbon-nitrogen ratio ranged between 27 and 79, and both had increasing values downwards in the peat profile. Unlike other measured elements that had highest concentrations in the topmost peat and litter, the total nitrogen values were highest (maximum value 2.1 % of dry mass) near the median WT in hummock samples.

3.3. Microtopography and vegetation

Based on statistical comparisons, the larger proportion of the surface area is low lying i.e. hollows or flat surfaces and smaller proportion hummocks (II). The range of forest floor surface level elevation differences in the transects and subplots were on average 80 cm and the mean surface elevation was 14 cm above the annual median WT. When comparing WT and ground surface elevation data, we found that more than half of the ground surface is above WT most of the year and even during the highest WT 8 % of the soil surface remains dry. We did not detect any difference between elevation changes in the two measured directions (towards the peat dome center and perpendicular direction). We also tested the differences between the two ground surface elevation measurement methods (transects and square plots) and found no significant differences in the results.



a)



b)

Figure 13. a) Forest floor water table levels in Natural Laboratory in a hollow in plot B based on long-term logger measurements. 0-level (solid horizontal line) is the annual median water table calculated from measurements during the period 1999–2005 excluding the exceptionally dry year 2002 (marked with *). Dashed horizontal lines show 10th, 25th, 75th and 90th percentiles. The mean soil surface elevation is in + 14 cm. Logger-data provided by Dr. Hidenori Takahashi. **b)** Kalampangan water table in the three blocks (wet, middle and dry) in year 2013. Soil surface is scaled to be equal to the figure a (mean soil surface elevation in block + 14 cm), and is defined separately for each block as the average of all plot corner leveling readings. Three solid horizontal lines show one year median WT for wet (highest line), middle and dry blocks.

When analyzing the occurrence of trees, saplings, seedlings, pneumatophores and pandans on the forest floor, we found that pneumatophores and pandans were generally located in the lower elevation than the other features. We also found that trees grew on higher grounds than saplings and saplings grew higher than seedlings. The number of seedlings on the forest floor was higher in comparison to saplings and trees. All the studied plots and transects had fairly similar features with high internal variation but small between sites variation.

3.4. Seedling growth and survival

During the measurement period in the years 2012-2014 (III, IV), the weather conditions were typical for the area with distinct wet and dry seasons. In the open degraded peatland in Kalampangan area, the changes in the WT were rapid and the median WTs lower in comparison to the Natural Laboratory forest but the range was fairly similar and stayed within 1 m during the measurement period (Fig 13).

In the experiments of 21 species without site preparation treatments in Kalampangan area (III), the growth and survival after 1.5 years varied greatly between the species. *Lithocarpus dasystachyus* (Miq.) Rehder had the best growth of 220 % and *Artocarpus integer* (Thunb.) Merr. the worst, -66 %, meaning that the average height of the seedlings declined during the measurement period caused by the death of the upper parts of the seedlings. Survival ranged between 94 % in *Shorea balangeran* and 22 % in *Palaquium leiocarpum*. Best performing species were *Shorea balangeran, Adenanthera pavonina* L., *Dacryodes rostrata, Horsfieldia crassifolia* (Hook.f. & Thomson) Warb. and *Lithocarpus dasystachyus*. Of the environmental variables, dry season and wet season had greatest influence both on the growth and survival. Studied species had great differences in the tolerance for continuously high WT during the wet season or drought during the dry season. We can nevertheless generalize, that drought inhibited growth more than continued high WT. On the other hand, survival decreased with wet season more often than with dry season.

Seedling height at planting had relatively minor effect on growth and survival in this study, possibly due to limited variation in the planting height. In several species, the increase in planting height reduced later growth, whereas in most species the increase in planting height increased survival.

Age of seedling was used in growth models to predict the future performance so that negative age parameter would indicate decline in growth in the future. In most cases, this parameter was either slightly positive or had no significance, thus this parameter had only minor importance in the models.

In the Natural Laboratory experiment (III), the small amount of seedlings prohibited possibilities for statistical comparisons. We thus only present some notes on the hydrology and seedling performance. Peculiar hydrology with very high changes in WT marked the environmental conditions in the area. Contrary to the situation in Kalampangan area, in the Natural Laboratory floodplain even during the dry season the WT stayed close to the soil surface. During the wet season, the whole river expanded to reach the forest edge and left the lowest lying planting areas 1.5 m underwater (Fig. 11). Floodplain is thus affected both by ombrogenous runoff waters from the forest during the dry season and the minerogenous river water during the wet season. Of the tested species, most of the seedlings of *Campnosperma squamatum*, *Adenanthera pavonina, Horsfieldia crassifolia*, and *Syzygium sp.* died during the wet season with a few survivors in the highest elevations inside the forest. On the other hand, most of the seedlings of *Dacryodes rostrata* and *Shorea balangeran* survived the wet season also in the lowest elevations and continued growing through repeated droughts and floodings. In comparison to Kalampangan experiments, the growth at the Natural Laboratory site was generally slower.

3.5. Effects of site preparation treatments

The three site preparation treatments (IV): weeding, fertilizing and mounding were tested in five species in the Kalampangan area (Fig. 14).

Seedling growth was positively correlated with weeding in all tested five species. On the other hand, weeding reduced survival in *S. balangeran* and *C. squamatum* but increased it in *A. pneumatophora*. In *D. polyphylla,* the results were mixed so that moderate weeding and total weeding had partly contradicting effects both on growth and survival.

Fertilizing was tested in three species and it had positive effects on all three: for *S. balangeran* and *A. pneumatophora* the growth was increased and for *A. pneumatophora* and *D. polyphylla* the survival was increased. The effect of fertilizing in seedling biomass and biomass allocation was tested in *S. balangeran* and *A. pneumatophora*. Both species had higher biomass and changes in biomass allocation with fertilizing with more pronounced

Figure 14. Nearly 2 m high *Shorea balangeran* saplings 22 months after planting only few days before the fires in September 2014 in fertilized and totally weeded (weeding ended in February 2014) plot in dry block in Kalampangan area with CIMTROP staff member Kris Yoyo.

results in *A. pneumatophora*. Allocation to roots decreased and to leaves increased in both species whereas the specific leaf area decreased in both species with fertilizing.

Mounding was tested in two species, *S. balangeran* and *A. pneumatophora,* in two blocks (middle and wet). In *A. pneumatophora,* the growth was positively correlated with mounding and in both species the survival was increased with mounding. The changes in soil temperature between mounds and ground surface were small. The clearest difference was observed in the diurnal temperature variation that was greater in the mounds than in the ground surface.

3.6. Effect of fires

The survival after fires (III, IV) was lowest in the dry block and highest in the wet block with high variation between the plots and species. The best survival of all species was in *S. balangeran* with survived seedlings in every plot. Weeding had positive effect on survival especially in the dry block. Also fertilizing and mounding had some positive effects on survival with less effect in the wet block. In general, the seedlings with high growth rate had better survival after the fire-event in comparison to the other seedlings.

4. DISCUSSION

4.1. Peat structure and chemistry

With our data set of surface peat samples (I), that was one of the largest by that date published, we could provide valuable knowledge on peat characteristics in the TPSF. This was also the first study to provide detailed information on peat characteristics in relation to the microtopographical features in the forest floor. While studying the TPSF peat, we made notes on the methodology of tropical peat research. Several of the sampling tools and techniques, such as the determination of the degree of decomposition used in peat research, are developed for boreal and temperate peatlands and are thus not well suited for tropical conditions (Stoneman 1997; Wüst et al. 2003; Page et al. 2004).

The structure of the tropical peat is much more varied than of boreal or temperate peats with particles of different sizes of undecomposed wood. With sometimes very loose surface peat mixed with abundance of leaf litter and living roots, we found the determination of the peat surface level somewhat ambiguous. We decided to use as the starting point the visible soil surface that is similar to the surface observed in remotely sensed data such as in Jaenicke et al. (2008) or Kronseder et al. (2012). Compaction of the peat during sampling was also common and our findings on peat bulk density values in the topmost peat were generally lower than in the previous literature (Kurnain et al. 2002; Page et al. 2004; 2011) that has in some cases neglected the top soil in bulk density calculations. Nevertheless, bulk density values and determination of the peat surface level together with the peat depth are of great importance in carbon storage calculations and accuracy in starting values is vital for reliable estimates.

The several burnt layers found in deeper peat especially in the plots near the river may indicate former human impact in the peatland area (Boehm and Siegert 2001). We found very well decomposed material from the topmost layers of hummocks but as it was mixed with undecomposed material, the overall decomposition degree in the surface peat was lower than in deeper peat. We suggested that the recently deposited litter on and inside the hummocks is more quickly decomposed than in the hollows, but the decomposed matter is also swiftly relocated downwards with the moving waters. In hollows in anoxic conditions, on the other hand, the decomposition can be expected to be slower, but the well-decomposed matter moving from higher surfaces raises the overall decomposition degree.

Within our sampling depth (70 cm) the occurrence of living roots didn’t show clear pattern of decreasing downwards, and we can assume that the lowermost living root zone lies typically deeper in peat. The biologically active zone in tropical peat may thus be fairly deep reaching up to 2 m depth (Weiss et al. 2002).

Our findings on ash content and mineral nutrient contents in peat were in line with previous findings (Neuzil 1997, Sajarwan et al. 2002, Weiss et al. 2002, Page et al. 2004). We also found that the carbon content is strongly influenced by the burnt material in peat. For generalizations of carbon content in larger areas, we suggest spatially large enough sample that would take into account the regional changes in carbon content in peat. In contrast to mineral nutrients, nitrogen concentrations did not decrease deeper in peat and we expect the nitrogen in deeper peat to be bound in more complex and stable forms that resist the decomposition process.

4.2. Microtopography and vegetation

Even though the study was conducted in one forest type, mixed swamp forest (Page et al. 1999), the variation in the forest floor structure was considerable between and within all our study plots (II). High amount of tree species with varying growth strategies combined with high biomass production rate (Kronseder et al. 2012) created innumerable situations on the TPSF forest floor adding to the structural complexity. Unlike in the boreal and temperate peatlands, we did not find any oriented patterning in the TPSF floor microtopography. There are several competing and complementing theories on patterning in boreal and temperate peatlands related to biotic and physical processes such as differences in *Sphagnum* growth rates (Nungesser 2003), hydraulic conductivity of the peat (Swanson and Grigal 1988; Couwenberg 2005), frost and ice action (Moore and Bellamy 1974) or scale-dependent feedback mechanisms between nutrient accumulation, peat accumulation and evapotranspiration (Eppinga et al. 2008). In the TPSF, the formation of the hummocks is very little studied (Shimamura and Momose 2005; Shimamura et al. 2006) but based on our observations the hummocks may originate from number of situations such as uplifted tree root systems, fallen tree trunks or aggregated pneumatophores. Decomposing wood and leaf litter piled on these higher surfaces form suitable substrate for the tree seedlings and root formation of the developing tree may further grow the hummocks. We nevertheless expect the processes behind the hummock-hollow variation to be complex and based more on random events related to tree mortality and litter production that are not likely to form any regular patterning, than to biological processes related to vegetation growth. Also the direction of water flow in such gentle sloping areas is less likely to have impact on the patterning (Couwenberg 2005; Eppinga et al. 2008; 2009; Dommain et al. 2010). With combined data from WT and surface elevation we could form detailed information of the duration of the annual WT situations on the forest floor. We can conclude that in the studied forest type, mixed swamp forest, the forest floor could be characterized as an irregular continuum of less common hummocks and more abundant flat low-lying surface where most of the peat surface is not inundated for most of the year.

In TPSF, the emergence of vegetation in relation to microtopography is influenced by a great variety of factors. More than 150 tree species (Waldes and Page 2002) with wide variation in niche differentiation (Freund et al. 2018) combined with the random factors of seed dispersion and natural disturbances create an endless variety of different situations on the forest floor. With our data we could not provide species-specific information on the habitat preferences. Nevertheless, we found that seedlings emerge in all ground surface elevations on TPSF floor, but bigger saplings and trees were concentrated on higher surfaces. We suggest, that competition on limited resources, in the case of TPSF especially on light and nutrients better available on hummocks, as well as limited tolerance to anoxic conditions on the flooded forest floor, favor tree growth on higher surfaces. Thus, even without a solid explanation on the dynamics steering the emergence of microforms on the TPSF forest floor and with very limited knowledge on TPSF tree species ecology, we expect the microtopography to serve an important function in the tree regeneration cycle.

4.3. Seedling growth and survival

Based on our findings on the 21 species experimenting (III), we could increase the knowledge of early stages ecology of several TPSF tree species. We for example increased the knowledge on the species' flood and drought tolerances, their suitability for different types of reforestation areas and suitable species-specific seedling height for planting.

Our test sites in Kalampangan had demanding conditions including high temperatures, heavy flooding and very limited nutrient supply in the soil for seedlings. In this experiment, we wanted to screen the potential of the species to grow and survive in these conditions that are relatively common in the degraded tropical peatlands. We did not perform any site preparation before planting. Depending on the species, the ground vegetation could have either provided shelter from intense light and high temperatures or suppressed the seedling by competition. With limited previous knowledge on the species ecology and keeping in mind the feasibility of the results for practical reforestation projects we also in this way decided to avoid probably unnecessary labor. Despite the harsh environment, some species had high survival and growth rates during the experiment and can thus be suitable for reforestation purposes. Because of the relatively short monitoring period, we cannot anyhow predict would the nutrient poor degraded peat support further growth of the seedlings. We also found that many of the tested species had poor records both in growth and survival and were clearly not suitable for primary species for reforestation in such conditions.

In the Natural Laboratory floodplain area, the environmental conditions differed from Kalampangan area especially in hydrology: river is flooding up to the forest during the wet season providing the area with water with supposedly higher nutrient and oxygen content in comparison to the ombrotophic peat areas in Kalampangan, and the constant water flow from the peat dome keeps the WT near the soil surface also during the dry season. Nevertheless, the seedling growth and survival were smaller in Natural Laboratory than in the Kalampangan experiment, possibly due to the long-term flooding and competition of the surface vegetation. Two species, *Shorea balangeran* and *Dacryodes rostrata*, had high survival rate after flooding and can be recommended for reforestation of similar areas. Reforestation of such marginal forests would form erosion reducing barrier and thus support sustaining the peat stores and vegetation of the adjacent forest areas.

4.4. Effects of site preparation treatments

Alongside with the species experimenting we conducted experimenting on site preparation treatments (IV). The species selection, combination of treatments and number of seedlings were affected by the seed availability and nursery success that was not in all cases optimal. It would have been for example worthwhile to do further testing with legume trees that could amend the soil nutrient status, such as *Adenanthera pavonina*, that is a nitrogen fixating tree and was used in experimenting in article III. Nevertheless, we derived valuable information on the five species responses to selected treatments. Based on the results, the increment in growth and survival can be substantial with the site preparation treatments of the right kind. Especially fertilizing during planting as a one-time effort was both effective and cost-efficient. Weeding was also favorable for the seedling success, but it was laborious and costly. Mounding may have benefits for certain species, but in this study it had relatively minor effect on the seedling success and was labor-intensive and costly. Of the studied species, *Shorea balangeran* had the best performance in all aspects, but it benefited only moderately from the treatments whereas *Alstonia pneumatophora* which had poor performance without treatments, had high tolerance to flooded conditions and can be recommended for reforestation if fertilized. Other relatively well performing species which can be recommended for reforestation purposes was *Dacryodes rostrata*. The problems in seedling availability and small seedling size at planting affected the results especially in the case on *Dyera polyphylla*. *Campnosperma squamatum* had relatively poor performance both in growth and survival and we would thus not recommend it as a primary species for TPSF reforestation.

4.5. Effect of fires

After the intensive main measurement period that lasted for one year, we had a plan to continue measurements on a lower frequency, once or twice a year depending on the resources (III, IV). This plan was interrupted by fires in September 2014 that caught all the three Kalampangan blocks and damaged the experiments severely. We nevertheless decided to measure the areas after the fire damage, in January 2015. Due to the varying intensity of the fires and differing edaphic and microclimatic factors, we cannot judge to what extent the survival after fires was coincidental or related to the real fire tolerance of the species. The random nature of fires prevented us also from making any statistical comparisons and thus the results have to be treated with caution. All species had the worst survival in the dry block and best survival in the wet block, but the differences between individual plots were great. In general, the good former height growth of the seedling seemed to increase its susceptibility to survive the fires. We found that especially weeding increased survival after fire as the removal of highly flammable surface vegetation may reduce the fire risks. The slight positive effect of mounding on survival after fires can be related to the reduced amount of highly flammable weeds near the seedling or that mound lifts the seedling above fast spreading ground fires. The recorded positive effect of fertilizing on survival may be related to the increased overall fitness of the seedlings. Nevertheless, without sufficient fire-prevention measures, and hydrological restoration that would keep the WT closer to the soil surface and reduce the risk of fire hazards, the vegetation restoration may not be likely to succeed.

4.6. Implications for TPSF restoration

In open degraded peatlands such as in the Kalampangan area, the environmental conditions are fundamentally different from the conditions in the natural TPSF such as in the Natural Laboratory area. In open degraded peatlands, the high temperatures, high light and rapid WT changes as well as reduced nutrient supply form litter and altered soil structure, set limits to the species success. Thus, the information on species growing environment in the natural TPSF is often not applicable as such but can be utilized as a reference point in the degraded TPSF ecosystem restoration.

Both in natural TPSF and degraded areas, the vegetation favors higher, e.g., generally drier, surfaces. Prolonged flooding can be fatal for seedlings, but especially in the degraded areas also the draughts and low WT can limit the survival. Thus, hydrological restoration that keeps the WT higher during the dry season is needed for reforestation actions.

In the natural TPSF, the gaps formed by fallen trees increase the light and space in the forest floor and add resources for tree regeneration, whilst stable temperatures and high air moisture content of the forest are maintained. In the degraded areas, where all taller vegetation is absent, existing low shrub- and fern cover cannot provide shelter, and temperatures and light can be too high for tree seedlings adapted to grow in forest conditions. Thus, for seedling success, there is a need for increased light in the natural forest, whereas in the open degraded areas there can be a need for shading. The tested weeding of the surface vegetation in the degraded area in this study was not mimicking the gap dynamics in the natural forests. Instead, weeding was a treatment adopted from agriculture and plantation forestry that has uses in reducing competition from surface vegetation and in the reduction of easily flammable fuel in fire-prone degraded peat areas, as proven in this study.

In the natural TPSF, the availability of recently deposited decomposing litter is sufficient for nutrient provision for growing vegetation whereas in the degraded areas nutrients are extremely limited. In the natural TPSF the hummocks with higher peat nutrient content in comparison to lower lying surfaces, are hotspots for vegetation regeneration, but in the degraded areas these features no longer exist. Forming artificial hummocks, mounds, which are both above the flooding and are fertilized can benefit seedling success in reforestation. The need for mounding in restoration is nevertheless strongly bound to the topography and ground water level limits of the specific area, as mounding will most likely not be useful in areas not prone to flooding.

When testing TPSF species for reforestation purposes in the field conditions, the previous information on species ecology in the undisturbed natural forest conditions has limited value and the testing may yield unexpected results. In the experiments in the Kalampangan area, we found for example that species that performed in the initial screenings of 21 species relatively poorly, benefited substantially from one time fertilizing at planting. Thus, one single operation can turn the failure into success. In addition, some of the tested species performed surprisingly well in the degraded area despite the harsh conditions very distinct from the natural forest conditions. This information could not have been derived from the descriptions of the species' typical habitats and ecology. Native pioneer species with high growth rates and possibly nitrogen binding qualities could be used to improve the conditions by quickly forming shade and improved soil for more demanding species, but information on the suitable species and techniques is lacking. For successful TPSF reforestation, there are still great gaps in the research and more monitored and reported field testing is needed for finding suitable species and techniques.

Finally, the vast spread fires have been extremely rare in the natural TPSF and the native vegetation of TPSF is not adapted to fire, whereas in the degraded areas fire is a common feature. For sustaining the peat stores and re-introducing the TPSF vegetation, the emergence of fires should be prevented.

5. CONCLUSIONS

In the first two articles of this study conducted in the natural forest in the Natural Laboratory in Sabangau, we have increased knowledge on TPSF ecology concentrating on peat soil properties, forest floor microtopography in relation to the water table, and vegetation positions in forest environment in the mixed swamp forest type. We found that the microtopography of the forest floor has no regular pattern. Nevertheless, the microtopography has an important role in the TPSF ecology. The conditions differ between the hummocks and hollows so, that higher surfaces, that have higher nutrient concentrations in soil and are less prone to flooding, are more occupied by vegetation.

In clear-felled, drained and burnt conditions, such as in the former MRP area, the hydrology, species composition, soil characteristics and microtopography of the peatland are thoroughly altered. In the third and fourth article of this study in the Kalampangan area, we concentrated on studying practical reforestation experimenting in degraded former TPSF areas. We increased knowledge on selected native tree species early stages seedling performance in degraded peat areas in relation to site characteristics, site preparation treatments and fires.

The global importance of the tropical peat ecosystems to carbon storage and biodiversity and their severe destruction call for ever more urgent restoration actions. Progressively increasing area of peatlands in SE Asia are converted and vast areas are in similar degraded state as the Kalampangan sites in this study. As in complex tropical ecosystems in general, it is doubtful that the high biodiversity of the natural TPSFs can be attained through restoration in the degraded areas in the near future. Therefore, the primary focus should be on restoring the ecosystem functions, such as water table regulation, stable microclimate provided by full canopy TPSF and increased litter production that may reinitiate the carbon accumulation to soil. In most cases this means both hydrological restoration and reforestation. For the first steps of reforestation, finding tree species that are tolerant to extreme and varying conditions prevailing in the degraded peatlands is a challenge. For reforesting areas characterized by particularly extreme water table fluctuation, similar to the Natural Laboratory floodplain, the flood tolerance of the seedlings becomes paramount. In the drier peat areas, similar to Kalampangan, the biggest efforts at the remediation of the situation should be targeted on fire prevention. In all cases, the target is also to find species that are fast growing and can improve the microclimate by shade provision for more demanding species and to find species that can improve the soil by nitrogen binding. We have experimented here with 21 species but research with widened selection of species, site types and techniques is needed for confirming success in reforestation set in practice. To gain better social approval, use of species providing non-wood forest products or other benefits for the local communities should also be considered. In this way, we may also increase the possibility for reforestation success in the long term.

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